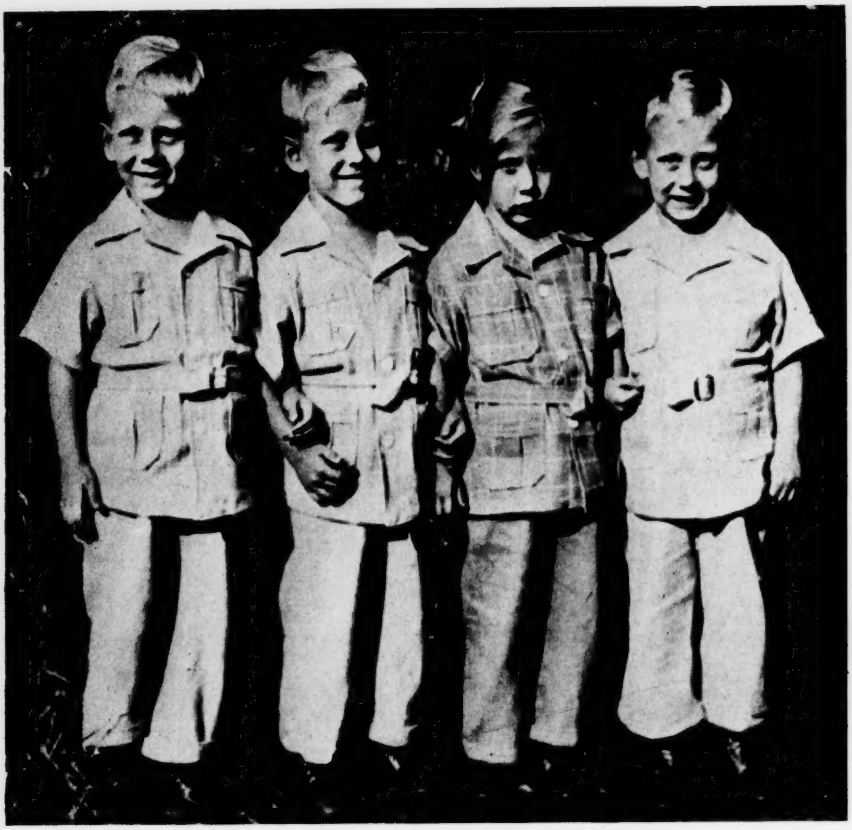
The Journal of HEREDITY



TWO KASPARS IN FOUR "PACKAGES"

(SEE PAGE 27)

Hereditary Cataract

Hybrids of Dallis Grass

Hybrid Frogs

VOLUME 34 JANUARY, 1943 NUMBER 1

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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CONTENTS

CORRESPONDING GENES IN SPOTTED FROGS
By John A. Moore 3

HEREDITARY CATARACT
By Sedgwick E. Smith and B. F. Barrentine 8

A USEFUL POLLINATION METHOD FOR WATERMELONS
By M. N. Walker 11

INTERSPECIFIC HYBRIDS IN THE GENUS *Paspalum*
By Glenn W. Burton 15

INHERITED FOOT-BLISTERING IN AN AMERICAN FAMILY
By J. L. Cartledge and Virgil W. Myers 24

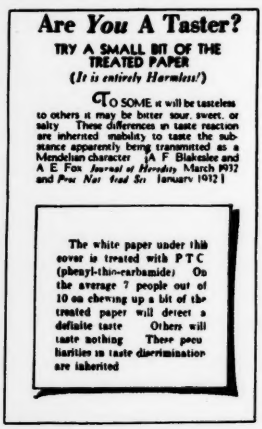
BOWED PASTERNS IN JERSEY CATTLE
By F. W. Atkeson, Franklin Eldridge and Heman L. Ibsen 25

THE KASPAR QUADRUPLETS
By H. H. Newman and Iva C. Gardner 27

Notes and Reviews

FAMILY FIXTURES (Rev. of WHITNEY: *Family Treasures*)
By S. J. Holmes 10

AN ACTIVITY-GENE IN THE ALBINO RAT 26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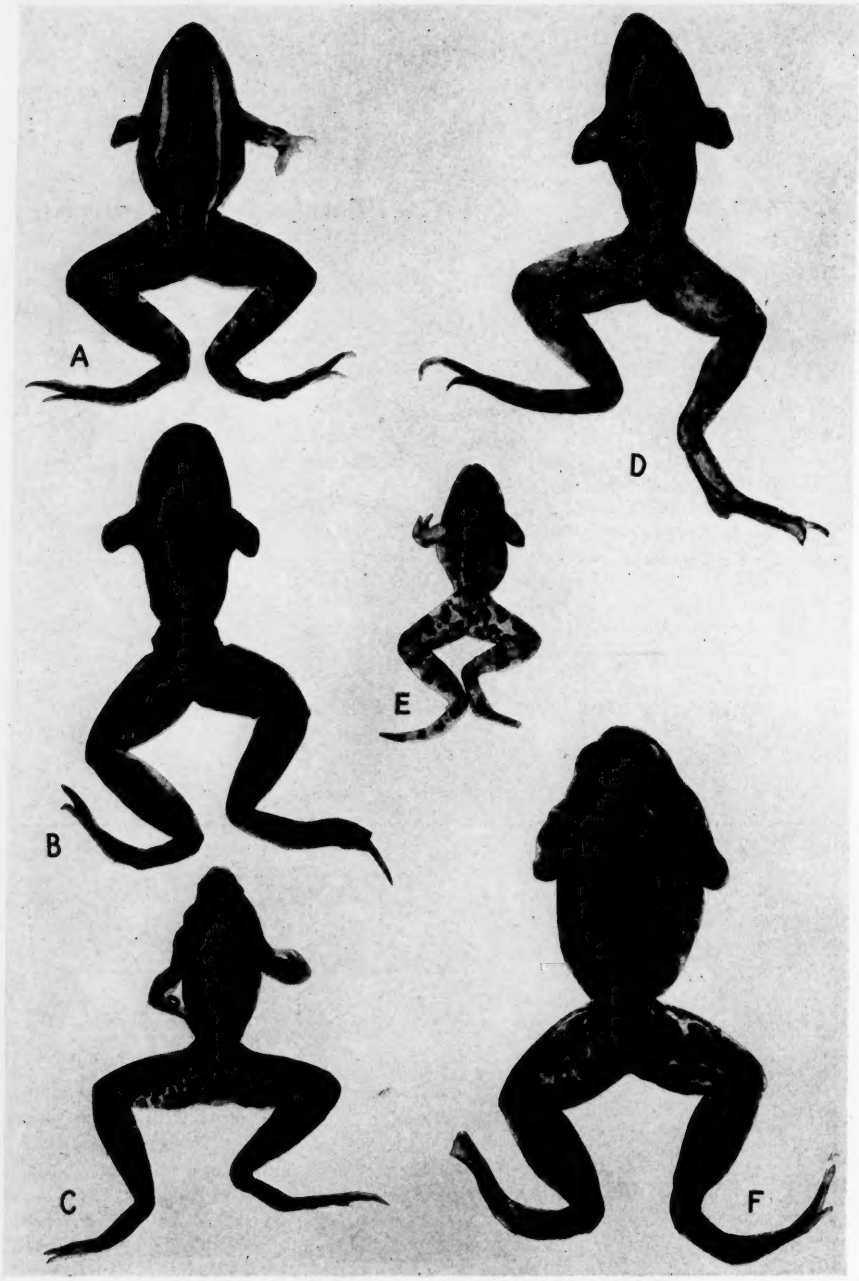


SPOTTING PATTERNS IN THREE FROG SPECIES

Figure 1

The bright green leopard frog (*Rana pipiens*) is one of most widely distributed North American species. Three geographical forms are shown here: *A*—from Wisconsin; *B*—from Vermont; and *C*—from Oklahoma. Two related species are also shown: *E*—*Rana palustris;* and *F*—*Rana areolata*. The dominant *burnsi* mutation of *pipiens* is shown at *D*. This suppresses the spotting on the back in all three species, which can be taken as evidence that all of the species have the normal allele of *burnsi* in common.

CORRESPONDING GENES IN SPOTTED FROGS

of the genus *Rana*

JOHN A. MOORE

Queens College and The American Museum of Natural History

THE term "corresponding gene" has been suggested for those cases in which genes in two species behave as alleles in their respective hybrids but where their behavior in meiosis in this hybrid is unknown.[3] The usual method for their detection is to cross two species, each of which is homozygous for a similar recessive character. If the offspring show the recessive trait the genes are corresponding.[4] In those cases where the recessive mutation has occurred in only one of the species, the appearance of wild type offspring from a cross of the pure recessive with the wild type of the other species would indicate, with much probability, that corresponding genes exist. The recognition of corresponding genes in different species depends, therefore, on the fortuitous ability of the species to be hybridized and the presence of suitable mutations. An opportunity of testing for corresponding genes was presented when it was found that *"Rana burnsi"* is a color mutatant of the leopard frog, *Rana pipiens,* and that this mutant produces viable hybrids with *Rana palustris* and *Rana areolata.*

Description of the Three Species

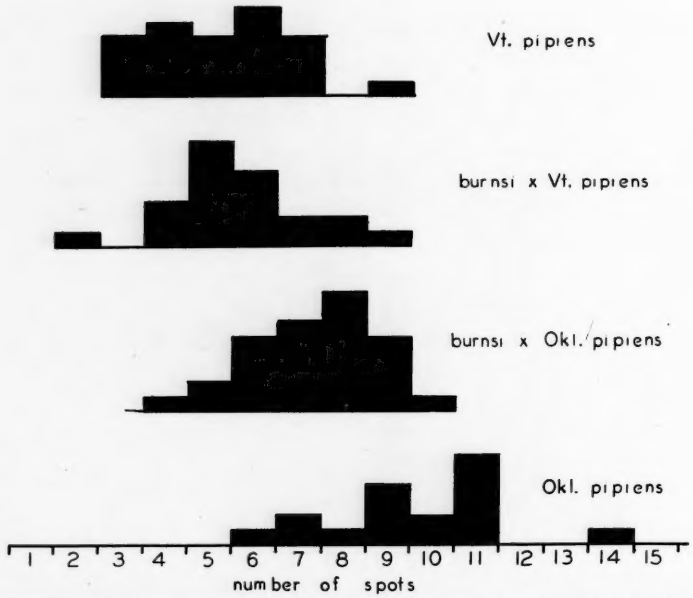
Rana pipiens has the most extensive distribution of any North American frog. It is found in most of North America east of the Sierra Nevada and in Central America. Throughout this range it exhibits considerable variation in pigmentation and to some extent in morphological characters. These variations have been dealt with in a variety of ways by taxonomists. Some have broken the population into separate species. Others have regarded the local variations as of subspecific value, while still others have maintained that the entire assemblage should be called *Rana pipiens.* All agree, however, that the variations are those of a single frog. The differences of opinion concern merely questions of nomenclature. In the present studies *pipiens* from Wisconsin, Vermont, and Oklahoma have been used. Individuals from Wisconsin (Figure 1*A*) and from Vermont (Figure 1*B*) are strikingly similar. The head is blunt and the back is covered by large dark spots. The Oklahoma specimens (*Rana sphenocephala* of most taxonomists) are smaller in size, the head is somewhat pointed, and the spots may be smaller (Figure 1*C*).

In western Wisconsin and Minnesota the populations of *Rana pipiens* contain an occasional individual that differs from the typical *pipiens* in lacking spots on the back (Figure 1*D*). This frog was described as *Rana burnsi* by Weed[5] but it has now been shown that the non-spotted condition is due to the presence of a single "dominant" mutation.[2] An individual heterozygous for this gene lacks spots on the back but invariably has them on the appendages. Homozygous individuals are devoid of black spots. A total of 25 *burnsi** collected in nature have been tested and all shown to be heterozygous for the gene.† When two *burnsi* are crossed a ratio of 3 *burnsi* to 1 *pipiens* is found in the offspring. A cross between *burnsi* and a typical *pipiens* results in a ratio of 1 *burnsi* to 1 *pipiens.*

The ranges of the other species used

*In this paper *Rana pipiens* carrying the *burnsi* gene will be referred to as *"burnsi"* for convenience.

†That no homozygous frogs have been found is probably explained by the scarcity of the non-spotted frogs in the population and the resulting small chance of mating with others of their own kind.



HISTOGRAMS FOR SPOT NUMBER IN NEWLY TRANSFORMED FROGS

Figure 2

The number of individuals (*"n"*), the mean (*"m"*), and the standard deviation (σ) for each group are as follows: Vermont *pipiens* — n = 24, m = 5.2, σ = 1.5; *burnsi* ♀ × Vermont *pipiens* ♂ — n = 21, m = 5.6, σ = 1.6; *burnsi* ♀ × Oklahoma *pipiens* ♂ — n = 28, m = 7.3, σ = 1.4; Oklahoma *pipiens* — n = 17, m = 9.7, σ = 1.9.

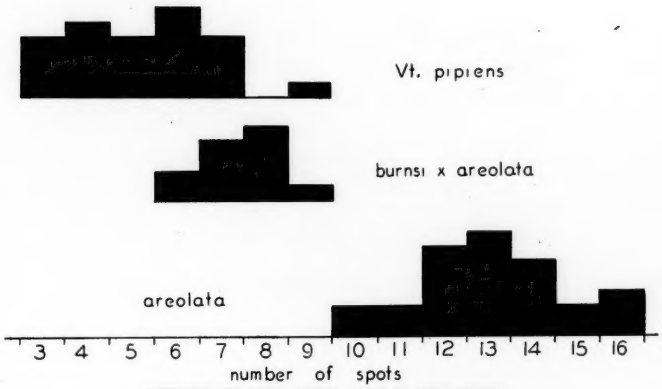
in these experiments, namely *Rana palustris* and *Rana areolata,* are included in the range of *Rana pipiens. Rana palustris* is found from James Bay south to the Gulf States, and west from the Atlantic to the plains. *Rana areolata* occurs in the Mississippi Valley region. *Rana palustris* (Figure 1*E*) resembles *Rana pipiens,* but it is a smaller species, characterized by dorsal spots which are larger and more nearly square, and by orange pigment on the ventral side of the legs. *Rana areolata* (Figure 1*F*) is the largest of the three. Superficially it bears little resemblance to the other species. The spots on the back are more numerous, the head is broad, and in body shape it looks somewhat like a toad. Nevertheless taxonomists have considered it to be closely related to the *pipiens* stock.

These three species, *Rana pipiens, Rana palustris,* and *Rana areolata* form viable hybrids (Moore[1] and unpublished data) that are intermediate in larval and adult characters. The ease with which these forms produce hybrids is itself an indication of their close genetic relationship.

Experiments

A single *burnsi* female was injected with pituitary and the resulting eggs were fertilized with sperm of: 1. *burnsi*; 2. *Rana pipiens* from Vermont; 3. *Rana pipiens* from Oklahoma; 4. *Rana areolata* from Oklahoma; and 5. *Rana palustris* from Massachusetts. In addition (6), eggs of *Rana palustris* were fertilized with sperm of *burnsi.* A total of 281 transformed young were secured. No difference in viability could be detected among the various crosses. The results of these experiments will now be given.

1. *burnsi* ♀ × *burnsi* ♂. This cross serves as a check on the heterozygosity of the *burnsi* ♀. Of a total of 45 young (Table I), 39



HISTOGRAMS FOR SPOT NUMBER

Figure 3

The number of individuals ("*n*"), the mean ("*m*"), and the standard deviation (σ) for each group are as follows: Vermont *pipiens*—n = 24, m = 5.2, σ = 1.5; *burnsi* ♀ × *areolata* ♂—n = 12, m = 7.4, σ = 0.9; *areolata* — n = 27, m = 13.1, σ = 1.6.

were non-spotted (*burnsi*) and six were spotted (*pipiens*). These results do not differ significantly from a theoretically expected ratio of 34 non-spotted to 11 spotted frogs (3:1). The female in question is therefore heterozygous (*Bb*) for the *burnsi* gene. In the hybrid crosses using this female and males of the other species, a ratio of one spotted to one non-spotted would indicate with much probability that the various spotted frogs have one corresponding gene in common.

2. *burnsi* ♀ × Vermont *pipiens* ♂. The male in this cross comes from a region where the *burnsi* mutant has never been recorded. Of a total of 56 young frogs, 23 were spotted and 33 non-spotted. These results do not differ significantly from the expected 1:1 ratio of 28 spotted to 28 non-spotted. In previous crosses between *burnsi* and *pipiens* from the same region in western Wisconsin, 196 offspring were non-spotted and 210 spotted in a total of 406.[2] It was concluded that the *pipiens* in question were recessive (*bb*) for the *burnsi* gene. The same conclusion can be drawn for the Vermont male.

3. *burnsi* ♀ × Oklahoma *pipiens* ♂. The male in this case is likewise from a region where the *burnsi* mutant is unknown. In contrast with the similarity of *pipiens* from Wisconsin and Vermont, specimens from Oklahoma differ, as previously mentioned, from the northern populations. The Oklahoma *pipiens* are known as *Rana sphenocephala* by many taxonomists. A total of 60 tadpoles transformed. Of these, 31 were spotted and 29 non-spotted. This 1:1 ratio indicates the Oklahoma male was of the *bb* genotype.

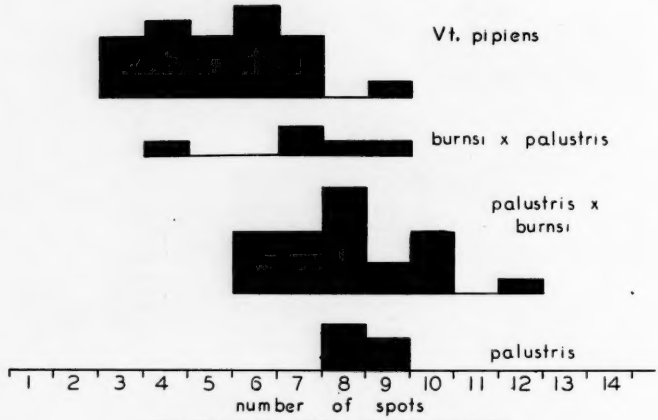
4. *burnsi* ♀ × *areolata* ♂. This cross is between unquestionably good species. It is of interest, therefore, to find the same 1:1 ratio in the offspring. A total of 52 young were secured of which 22 were spotted and 30 non-spotted. The dorsal pigmentation is suppressed by the *burnsi* gene of *Rana pipiens* in this distinct yet related species in the same way that it is suppressed in typical *pipiens*.

5. *burnsi* ♀ × *palustris* ♂. This is also a cross between related but definitely distinct species. This experiment was begun with 18 eggs and 10 of the resulting tadpoles transformed. Half of these were spotted and half were non-spotted.

6. *palustris* ♀ × *burnsi* ♂. Of the 58 from this cross 33 were spotted and 25 non-spotted. Combining these with the results of the above cross (5) a total of 38 spotted and 30 non-spotted frogs were obtained from the crosses between *palustris* and *burnsi*.

These crosses of the *burnsi* mutant with *areolata*, *palustris*, or typical *pipiens* from several localities all resulted in a ratio of one spotted to one non-spotted frog in the F_1. This agreement in genetic behavior is strong evidence* that these three species possess one corresponding gene locus in common. This locus is concerned with the presence of spots on

*There is always the possibility that the *burnsi* gene represents a duplication such as Bar in *Drosophila*. For this reason the crosses reported are not conclusive proof of a corresponding gene in the three species.



HISTOGRAMS FOR SPOT NUMBER

Figure 4

The *burnsi* ♀ × *palustris* ♂ and *palustris* samples are too small to be useful for purposes of comparison. The number of individuals ("*n*"), the mean ("*m*"), and the standard deviation (σ) for the other groups are as follows: Vermont *pipiens* — n = 24, m = 5.2, σ = 1.5; *palustris* ♀ × *burnsi* ♂ — n = 22, m = 8.1, σ = 1.5.

the dorsal surface of the frog. The "wild type" in the three species is a pure recessive (*bb*).

Pigment Differences in the F_1

Although the crosses between *pipiens* carrying the *burnsi* gene and *areolata, palustris,* or *pipiens* all result in a ratio of one spotted to one non-spotted individual, differences do exist in the pigmentation of the *spotted* offspring. Thus spotted frogs from the cross *burnsi* ♀ × *areolata* ♂ differ from the spotted F_1 in the *burnsi* ♀ × *palustris* ♂ cross. This might well be expected since the spotted frogs in the former case are hybrids between *pipiens* and *areolata,* and in the second case between *pipiens* and *palustris.*

The pigment differences that distinguish adult *pipiens* of the northern states (Vermont and Wisconsin) from those of Oklahoma are already present in recently transformed young. The average number of spots for Vermont young is 5.2 and for Oklahoma young 9.7 (Figure 2). Not only is there a difference in the number of spots but those in Oklahoma individuals are frequently smaller and more elongate. The dorso-lateral fold is lighter in the Oklahoma young. The spotted frogs from the cross *burnsi* ♀ × Vermont *pipiens* ♂ are, as would be expected, indistinguishable from Vermont *pipiens* young. The spots are large and the average number is 5.6. The average for the spotted young in the cross *burnsi* ♀ × Oklahoma *pipiens* ♂ is 7.3, a value roughly intermediate between the average for the Vermont and Oklahoma controls. The spots in these hybrids are intermediate in size and the dorso-lateral fold is light in color as in the Oklahoma frogs (this condition is also apparent in the non-spotted young from this cross). Histograms for spot number are given in Figure 2. The data for Vermont and Oklahoma *pipiens* are from experiments conducted concurrently with those reported here.

Marked differences in the type and number of spots exist between Vermont *pipiens* and *areolata.* The *areolata* young have more numerous and smaller spots than the Vermont *pipiens* young. The average number for the Vermont *pipiens* is 5.2 and for the *areolata* 13.1. The *areolata* characteristically have many tiny spots among the large ones and there is a tendency for the main spots

to be opposite in the young. The spotted young from the *burnsi* ♀ × *areolata* ♂ cross show an increase in the number of spots over the average for the Vermont *pipiens*—the average for these hybrids being 7.4 (Figure 3). The spots themselves are intermediate between the two parent types in respect to size. These F_1 hybrids resemble *areolata* in having many small spots among the major ones. The large spots tend to be opposite as in *areolata*.

Recently transformed *palustris* differ from *pipiens* of the same age in having rectangular instead of round spots. These rectangular spots are usually larger, more numerous, and arranged opposite one another in two parallel rows. It will be recalled that the average number of spots in the Vermont *pipiens* is 5.2. In the *palustris* ♀ × *burnsi* ♂ cross the average number of spots was 8.1. In the five *palustris* controls which transformed, three had eight spots and the other two had nine. This small number of *palustris* controls does not permit adequate comparison of the number of spots between the hybrids and *palustris*. In the reciprocal cross, *burnsi* ♀ × *palustris* ♂, five spotted young were available for counts. Of these one had four spots, two had seven, one had eight, and one had nine. Some striking differences were noticed in the form and arrangement of the spots. In the spotted young of *burnsi* ♀ × *palustris* ♂ the individual spots were as large or larger than in *palustris*, and therefore much larger than in *pipiens*. As in *palustris* the spots tend to be opposite one another. In the *palustris* ♀ × *burnsi* ♂ young the spots were somewhat smaller and less regular in outline and arrangement, thus resembling *pipiens*. In comparing these two groups of reciprocal hybrids it appears that the form and arrangement of the spots resembles the paternal species more closely than the maternal species. This relation, as a matter of fact, is of frequent occurrence in hybrid frogs (Figure 4).

Summary

Rana pipiens heterozygous for the dominant *burnsi* gene has been crossed with *pipiens* from localities where the *burnsi* mutant is unknown, with *Rana palustris*, and with *Rana areolata*. The *burnsi* mutant causes the suppression of the dorsal spots. The F_1 in each cross shows a ratio of one spotted to one non-spotted frog. These results are good evidence that the three species have one corresponding gene in common.

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TABLE I. Results of Crosses.

	burnsi × *burnsi*	*burnsi* × Vt. *pipiens*	*burnsi* × Okl. *pipiens*	*burnsi* × *areolata*	*burnsi* × *palustris*
Spotted	6	23	31	22	38
Non-spotted	39	33	29	30	30
Deviation	5.25	5	1	4	4
St. error	2.9	3.7	3.9	3.6	4.1

HEREDITARY CATARACT

A New Dominant Gene in the Rat

SEDGWICK E. SMITH* AND B. F. BARRENTINE†

IN 1941 it was observed that an adult female rat in the colony of the Laboratory of Animal Nutrition, Cornell University, had bilateral cataracts. That this character was hereditary was evident when several of her subsequent offspring developed cataracts. A series of matings were planned to establish the mode of inheritance which, with other observations, are presented herein.

Bourne and Gruneberg[2] have described a degeneration of the retina and cataract in the rat. This is due to a recessive gene which along with other differences clearly differentiates this character from the one here described. A review of the literature relative to hereditary cataracts is given by Bourne and Gruneberg and will not be repeated here.

Description of the Defect

The cataracts are evident at the time the eyes are first opened at about 14 days of age. Usually both eyes show cataracts at this time, but in a few instances, one eye did not show macroscopically evident cataract until a few days later. The cataracts were usually complete or mature when first seen, but in some instances only the center of the lens was affected. This rapidly spread to form a complete cataract in a few days. In every case so far examined both eyes developed cataracts. The rats were, of course, completely blind, but in spite of this, they were vigorous, grew normally and reproduced. Though detailed studies were not made of the degree of fertility, it appeared that there was more sterility among cataractous than among non-cataractous rats.

In order to ascertain how long before the opening of the eyes the cataracts developed, young from a homozygous cataractous female were sacrificed at daily intervals following birth. Cataracts were first observed in a four-day old rat. Cataracts were not definitely seen in rats younger than this. It would thus appear that the cataracts develop shortly after birth.

In removing some of the lenses for chemical analyses it was noted that cataractous lenses were definitely smaller and lacked the plump shape of normal lenses. Instead of being globular, the cataractous lenses were shaped like a mushroom.

Chemical analyses as well as X-ray pictures of the lenses showed that the opacity was not due to calcification nor to other mineral deposits, since the ash content of cataractous lenses was no higher than that of normal lenses. The lens opacity is probably due to a precipitation of the lens protein, as is the case in most human cataracts.[1] The eyes of ten cataractous rats ranging in age from three weeks to three months were serially sectioned, stained with hematoxylin and eosin and examined microscopically. In no instance was any anatomic abnormality found. The retinas were normal in every respect. Since parathyroidectomy[5] and diabetes[6] predispose some animals to cataracts, microscopic examinations were made of the parathyroid glands and the pancreas. Both organs were normal in every respect. The blood glucose of cataractous rats was within normal variation.

Genetic Analysis

A cataractous male rat of our stock (Osborne-Mendel) was mated to three normal females of an unrelated strain

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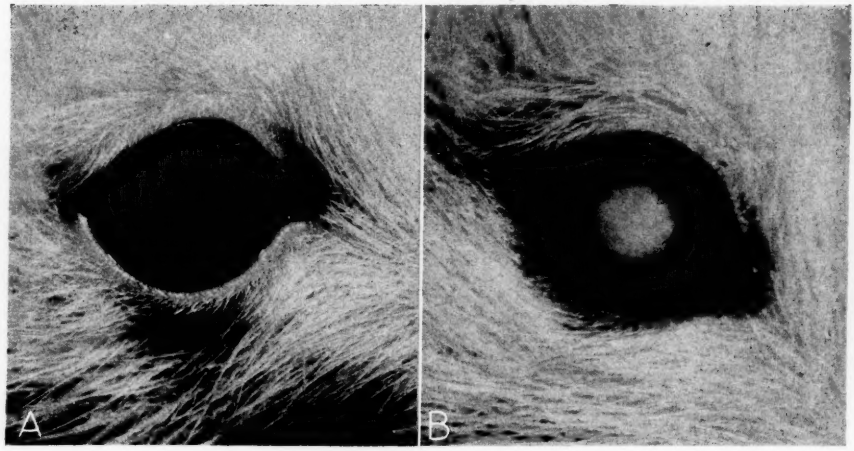

NORMAL AND AFFECTED EYES
Figure 5

A—shows the normal eye of a rat, and *B*—the eye of a rat having a cataract. The cataracts are conditioned by a dominant gene.

(Long-Evans). From these matings 32 young were born of which 15 had normal eyes and 17 had cataracts. This close approximation to a 1:1 ratio indicated that the cataract was produced by a simple dominant gene. Furthermore, these matings showed that the gene was autosomal, since the cataracts were evenly distributed between male and female offspring. If the gene were sex-linked, all male offspring would have been normal. Several cataractous rats, each of which had one normal parent, were mated *inter se*. The results of these matings were 39 cataractous and 15 normal young, a close approximation to a 3:1 ratio. Several other cataractous rats, each of which had one normal parent, were mated to normal rats. From these matings 73 cataractous and 71 normal offspring were secured, nearly a perfect 1:1 ratio. Eight cataractous rats secured from cataract × cataract matings were tested for homozygosity by mating them to normal rats. Homozygosity was assumed, if such cataractous rats had 20 or more offspring all of which had cataracts. Of these eight rats, three proved to be homozygous and five heterozygous, which fiits the expected ratio of 1:2. The cataract is thus caused by a simple dominant and autosomal gene which we designate as *Ca*.

Discussion

While the etiology of this cataract would be of considerable interest, our efforts to date to determine the underlying physiologic or anatomic defect have been unfruitful. A number of dietary deficiencies have been shown to cause cataracts,[3,4,8,9,10] but this would not appear to be the case with this hereditary cataract for all rats were maintained on an adequate stock colony diet.[7] The possibility that these cataractous rats were unable to assimilate an adequate diet completely is, of course, not ruled out.

Summary

A new simple, dominant and autosomal gene *Ca* is described in the albino rat. Tihs gene brings about bilateral, complete cataracts in young rats, starting at a few days after birth.

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FAMILY FIXTURES

IT is not necessary for John Doe to *read* this volume* to be strongly impressed with the potency of human heredity. All he needs to do is to look at the pictures. There are 234 figures, most of which are photographic reproductions illustrating the occurrence of similar characteristics in two or more members of a family. The selection is confined to normal traits such as stature, obesity, head form, shape of ears, peculiarities of the eyes, number, shape and jointing of fingers and toes, form, color and arrangement of hair, shape of nose, and many other features except those which are obviously pathological. Through the wealth of photographic reproductions, most of which are very clear, the facts of heredity make a direct appeal to the eye. They stare one in the face in nearly every page. In most books illustrations are subsidiary to the text, but here the text is mostly explanatory of the figures.

In a few cases the iconographic method is carried beyond the point of utility. Pictures of more than one member of a family distinguished for musical ability or the lack of it, the possession of artistic talent, or ability in literary expression convey no information about heredity in the present state of our knowledge of physiognomy. This, however, is a very minor criticism especially in view of the not uncommon custom of inserting illustrations with no other apparent purpose than to cheer up the reader.

I would not convey the impression that Dr. Whitney's volume is little more than a picture book. The author explains that his book "is written for amateurs." The pictures tempt the reader to peruse the comments in the text. Most people are curious as to the inheritance of the characteristics they observe and when the facts of heredity are pictorially presented to them they will naturally want to learn more about them. But in addition to supplying the reader with much interesting information concerning the inheritance of individual traits, Dr. Whitney gives a simple, clear and scientific account of the general principles of heredity and corrects a number of misconceptions of the subject which have become widely current. His book is well adapted to awaken interest in the inherited peculiarities of human kind and to prepare the reader for tackling more pretentious treatises.

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University of California

*Family Treasures: A Popular Guide to Heredity, by D. D. Whitney, The Jaques Cattell Press, Lancaster, Pa., 1943.

A USEFUL POLLINATION METHOD FOR WATERMELONS

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SINCE watermelons are normally cross-pollinated and since the chief criterion of value of the crop is the appearance and quality of the mature fruit, it is necessary to carry out wholesale self-pollination to insure adequate material for selection when the melons are cut. To be satisfactory on such a scale, a pollination method must be rapid and easy; it must give full protection against contamination, and must cause as little injury to the blossoms as possible. Such a method has been developed and has been very useful in watermelon breeding work at Leesburg, Florida, for the past ten years.

None of the methods heretofore described for pollinating watermelons has proved so rapid or simple as that we are using. Large paper bags have been widely used in watermelon breeding in Iowa and California,* but they proved to be impractical under Florida conditions. Heavy dews made them difficult to handle, and they were blown about by the wind, extensively injuring blossoms and vines. Small glassine bags were difficult to use without injuring or breaking off blossoms, and they were inclined to sweat and thus cause excessive rotting of female blossoms. Small cloth bags with draw strings, used at the California Experiment Station,* also were prone to injure the blossoms. When they were wet with dew the draw strings were especially difficult to release without snapping off the blossoms.

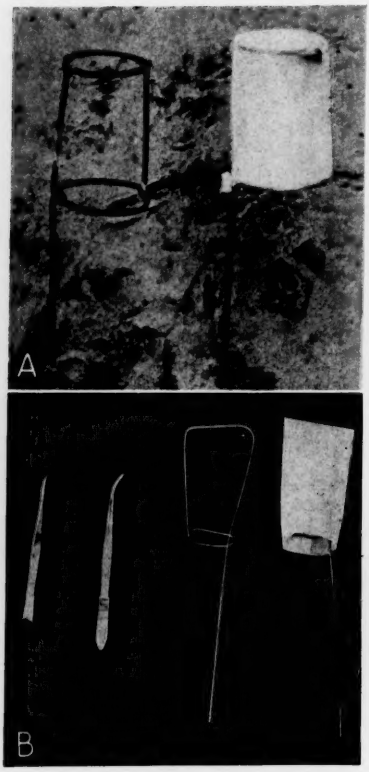
The method used in Florida was devised to speed up the work, to avoid contact with blossoms and to maintain the normal environment under blossom coverings as far as possible, and to anchor vines to prevent excessive wind injury. The latter point has been of especial importance, since the repeated use of soil made it difficult to maintain sufficient trash to anchor the vines.

To accomplish these purposes small cloth-wire cages were constructed, as shown in Figure 6*A*. The frames for the cages were approximately two inches in diameter and three inches long, with the wire on one side of the frame extending four to five inches to serve as a means of anchoring the cage to the ground. A slightly smaller diameter at the top made covering of the frames somewhat easier. The wire used was 14-gauge galvanized smooth wire, and all joints were soldered. Small bags made of coarse, unbleached muslin were used in covering the frames. This material permitted circulation of air with a consequent reduction of temperatures within the cages. Although the initial cost of construction was rather high, ten to twelve cents, it was found that with reasonable care the cages were usable for five or more years before recovering was necessary. This type of cage was used over both male and female blossoms. In all operations incident to pollination they can be quickly and easily removed without injuring the flowers. The cages are strong and light, and as many as 100 may be carried in an ordinary market basket.

After blossoms became numerous three or four men bagged 600 to 800 female blossoms and the accompanying males in an afternoon on an area of eight to fifteen acres. Only the most vigorous female flowers were bagged. Pollinations were made the following morning at the rate of 50 or more an hour, depending on how widely the marked blossoms were scattered.

Actual pollination was done with curved forceps. After the male blossom was removed from the vine it was held

*Porter, D. R., Watermelon Breeding. Hilgardia 7: 589: 592. 1933.



WATERMELON BREEDER'S TOOLS

Figure 6

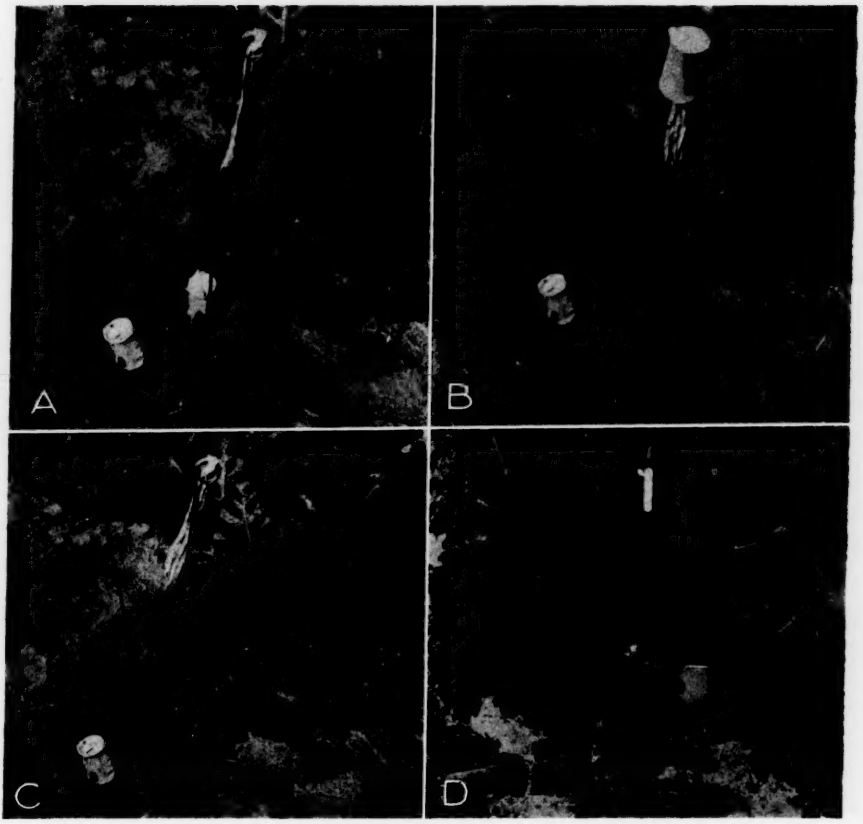
A—shows the frame and covered cage used for pollinating watermelon flowers. *B*—shows a glassine covered frame for use over male blossoms, and type of forceps used in handling these blossoms.

by the receptacle with blunt-tipped forceps, while its petals were stripped off with the sharp-tipped forceps.

Wire stakes were useful for marking the blossoms, since the stakes could be conspicuously tagged and 40 or 50 could be carried in one hand. These were made of number eight or ten gauge galvanized wire, 36 inches long and with a small ring about one inch in diameter at one end. Blossoms to be pollinated the following day were marked with these stakes with small pieces of cheesecloth tied in the rings (Figure *7A*). When the pollination was completed, the small cage that had been used to cover the male blossoms was placed on top of this stake to indicate that the pollination had already been made (Figure *7B*). As soon as all blossoms were pollinated another wire stake was placed near each pollinated blossom and the cage over the flag was picked up (Figure *7C*). Any tagging of blossoms was done at the same time. Twenty-four to thirty-six hours later the flagged stake and the bag over the female blossoms were picked up, thus leaving one wire stake to mark the pollinated blossoms. Tags were not placed on these stakes until the melons were definitely set (Figure *7D*), except when crosses were made or when it was desired to indicate the date of pollination. This procedure allowed the maximum number of selfings to be made during the early morning hours when conditions for pollination were most favorable. As a rule, all flowers marked one afternoon could be pollinated before nine o'clock the following morning. When the male parent was the same as the female, all pollinations made on a particular day were marked by inclining the stakes over the pollinated blossoms pending more definite marking.

No contamination was detected during a period of ten years, even though in many cases the cages did not make close contact with the soil. In the earlier work an effort was made to insure very close contact between the lower edges of the cage and the soil. Later this was found unnecessary, and as long as the blossoms were well covered no especial effort was made to seal all of the lower edge. The lack of contamination was apparently due to the fact that bees were practically the only agent of outside pollination, and they always approach the blossom from above. In the early morning it was easy to detect female blossoms that were pollinated by any outside agency because at that time small quantities of pollen were visible to the naked eye. The same method was satisfactory in cantaloupe breeding and probably could be used with cucumbers.

Other workers who have used the cages described above have made small changes in its form and some of these might help in reducing the initial cost.



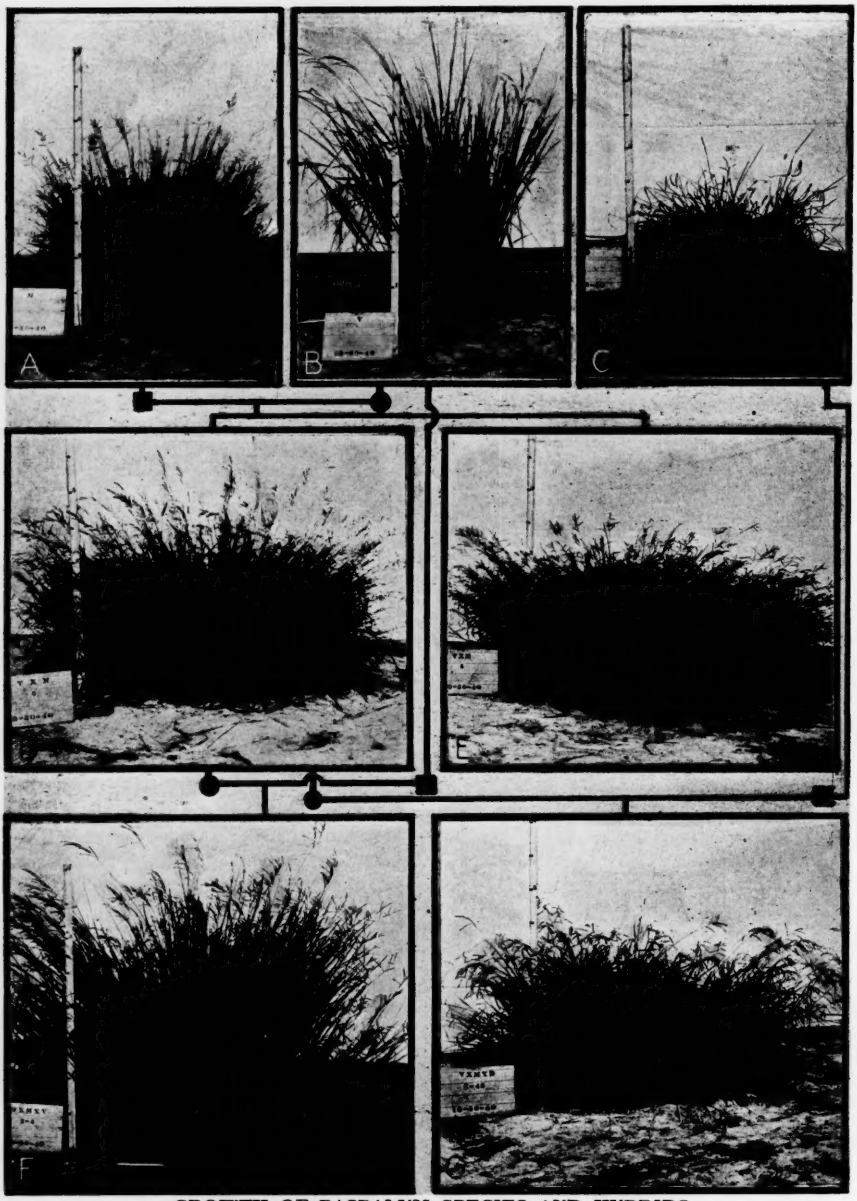
POLLINATING CYCLE

Figure 7

A—Male and female blossoms covered and marked for pollination. *B*—Cage removed from male blossom and placed on top of stake after pollination. *C*—Bag for male blossom has been picked up and record stake set. *D*—Tagged stake indicating selfed melon; this tag is attached to melon when harvested.

One of these was the use of a single piece of wire the upper part of which was coiled into a spiral shape to hold the bag. Another adaptation of the same method, and one which might be used throughout, is illustrated in Figure 6*B*. Cages of this type may be more quickly constructed than the one first described, but they would have to be made somewhat larger than the one illustrated. The type shown was used with small glassine bags solely on male blossoms where the cages did not remain on longer than twelve to fifteen hours. Where a few pollinations are to be made wax paper cups may be used with a hooked wire about six inches long inserted through the bottom of the cup with a hook over the rim of the cup.

Large gelatine capsules proved useful for pollinating in the greenhouse. The smaller end was used over the male blossoms and the larger one over the female blossoms. The capsules on the female flowers were used with the petals when they withered. It was not possible to use these capsules out-of-doors, however, as dews or rains softened them.



GROWTH OF PASPALUM SPECIES AND HYBRIDS

Figure 8

The total seasonal growth of representative plants of species and hybrids is shown. The upper row shows: *A—Paspalum malacophyllum; B—P. urvillei; C—P. dilatatum.* Below these plants are shown four hybrids of various ancestry. The second row shows two hybrids of *P. urvillei* × *P. malacophyllum,* Hybrids No. 3 and No. 5. A backcross of one of these hybrids to *P. urvillei* is shown at *F* and a triple hybrid including *P. dilatatum* at *G.* Marked hybrid vigor was shown by most of the hybrids.

INTERSPECIFIC HYBRIDS IN THE GENUS *PASPALUM**

GLENN W. BURTON†

IN lowland areas on the more fertile soils in the Southeast, Dallis grass (*Paspalum dilatatum* Poir.) probably ranks first among the improved grasses that may be used in permanent pastures. Although much seed is planted annually, comparatively few good stands are obtained even with rather heavy seedings. A primary factor responsible for this high seed mortality, and for the high prices the seed commands is the seed destroying disease, ergot (*Claviceps paspali* Stevens and Hall). The frequent occurrence of ergot on Dallis grass in the United States and the failure to find practical and effective control measures have made breeding for ergot resistance the principal objective in the improvement of this grass.

In a South Georgia survey made in 1936, occasional isolated plants of Dallis grass growing along roadsides were found to be free of ergot but all plants in pastures or rather dense plantings were heavily infected. In 1937 some 4,000 Dallis grass seedlings coming from commercial seed lots, and the isolated plants found to be free of ergot in 1936 were quite uniformly infected with this disease. Thus attempts to obtain resistance by simple selection within large populations of Dallis grass offered little promise of success. Later studies of populations obtained from Australian seed lots reported to be resistant led to the same conclusion.

In various plantings where several of the *Paspalum* species had been closely associated, Vasey grass (*Paspalum urvillei* Steud.) had shown considerable resistance to ergot and *Paspalum malacophyllum* Trin., an introduction from Argentina, had appeared to be immune to this disease. Cytological investigations of these *Paspalum* species[1,2,3] revealed that all three mentioned above possessed 40 chromosomes as the *2n* number. Nevertheless, many experimental attempts to hybridize Dallis grass with Vasey grass or *P. malacophyllum* have failed.

In 1937 a quantity of seed was harvested from a single Vasey grass plant growing in the midst of a Dallis grass planting and approximately 50 feet from a planting of *P. malacophyllum*. It was believed that a study in 1938 of some 5,000 seedlings from this plant would give an index of the genetic variability of Vasey grass when selfed and might reveal that the desired hybrids with Dallis grass had been made by natural crossing in 1937. No Vasey × Dallis grass hybrids appeared but five unusual plants were found. Since Vasey grass was the female parent of these plants and since the floral characteristics of these plants resembled *P. malacophyllum* much more than any other possible male parent (see the descriptions that follow) there could be little doubt but that they were hybrids between Vasey and *P. malacophyllum*. Hybrids that have since been made between these two species under controlled conditions prove that the assumed parentage of these natural hybrids was correct. Fifty-seven (Vasey × *P. malacophyllum*) × Vasey hybrids, 100 (Vasey × *P. malacophyllum*) × Dallis grass tri-hybrids, and several hundred plants identical with the female parent were obtained by pollinating these male-sterile Vasey × *P. malacophyllum* hybrids with Vasey or Dallis grass pollen.

In order to facilitate a quantitative comparison between some of these hy-

*Cooperative investigations of the Division of Forage Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, the Georgia Coastal Plain Experiment Station, Tifton, Ga., and the Georgia Experiment Station, Experiment, Georgia.

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brids and their parents the following experiment was designed: In the fall of 1939, ten clones of each of the following species or hybrids were planted in 6-inch glazed pots in the greenhouse: *Paspalum urvillei* (*V*), *Paspalum malacophyllum* (*M*), *Paspalum dilatatum* (*D*), *V* × *M* No. 3, *V* × *M* No. 5, (*V* × *M* No. 3) × *D* No. 6-63, (*V* × *M* No. 3) × *D* No. 7-42, (*V* × *M* No. 3) × *V* No. 2-4, and (*V* × *M* No. 3) × *V* No. 2-7. On April 26, 1940, the nine most uniform plants of each of the nine clones, now well sodded, were removed from the pots and were planted eight feet apart in each direction in a well drained Tifton sandy loam to permit an expression of their growth when free of plant competition. The experiment was set up on a factorial design to test the effect of three levels of fertility and three cutting treatments upon the nine clones of grass.

Most of the comparisons appearing in Tables I and II were made on the parents and their hybrids in this planting. The measurements for any one character for all of the grasses treated were made at one time on plants uniform in age and treatment. Only mean measurements are presented.

Root tips of the parents and hybrids were fixed in Craf fixative, embedded in paraffin and the 10 μ sections were stained by the iodine-gentian violet technique. Camera lucida drawings of the chromosomes at the equatorial plates in these root tip cells are shown in Figure 10.

The total seasonal production of dry matter made by these hybrids and their parents when cut weekly, every six weeks and only once late in the fall was determined in 1940 and 1941 and appears in Table III.

At weekly intervals from August 14 to October 23, 1940, all ripe seed heads were harvested from each of the three plants of each grass not cut until October 30. The heads were then threshed and the production of florets and the percentage of florets containing caryopses were determined for each harvest from each plant. Significant seasonal variations in the percentage of florets to set seed were noted for all of the grasses in this test. The weekly determinations have been combined in Table IV to give the average percentage of florets setting seed and the total production of caryopses for each grass for the period from August 14 to October 23.

Vegetative Characteristics

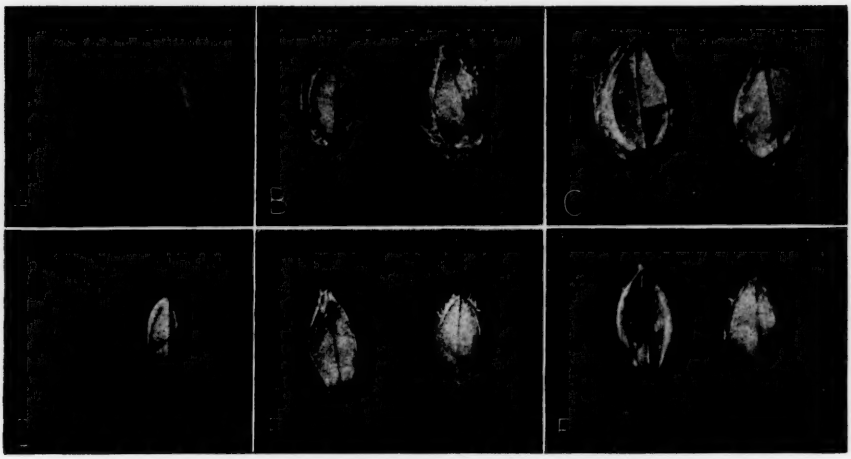
The appearance of representative mature plants of the three parent species and their hybrids used in this test is shown in Figure 8. These photographs together with the data in Tables I and III indicate that the hybrids included in this study were more vigorous than the parent *Paspalum* species.

It is interesting to note that *V* × *M* No. 5, due to its more prostrate stems and rooting nodes, spread much faster than any of the other grasses compared with it in Table I. The failure to find any evidence of the prostrate habit in large selfed populations of both parent species suggests that the prostrate habit of *V* × *M* No. 5 may be a case of complementary factor inheritance. The difference between the average spread of the two *V* × *M* hybrids, No. 5 and No. 3, far exceeded the one per cent level of significance.

Although Dallis grass was the least succulent of all of the strains in the fall harvest (because it was almost completely dead) the (*V* × *M*) × *D* hybrids were significantly more succulent, lower in dry matter, than any of the other hybrids or species in this test. That the two representatives of each hybrid combination were so similar in dry matter percentage is worthy of note.

The rating on the coarseness of stems in Table I indicates that the (*V* × *M*) × *V* hybrids and Vasey grass were coarse; Dallis grass and the other hybrids were similar and intermediate and *Paspalum malacophyllum* was fine-stemmed.

The hairiness of the leaves of these grasses is not as uniform and constant as many plant characters. Usually, however, the hairiness ratings presented in Table I adequately describe the leaves



SPIKELETS OF PASPALUM SPECIES AND HYBRIDS

Figure 9

Two views of the spikelets of: *A—Paspalum malacophyllum; B—P. urvillei; C—P. dilatatum; D—P. urvillei* × *P. malacophyllum; E—P. urvillei* × *P. malacophyllum* × *P. urvillei;* and *F—P. urvillei* × *P. malacophyllum* × *P. dilatatum.* × 6.

of these grasses and may be used to assist in their vegetative identification. Hairiness of the leaf blade margin on mature leaves and of the upper surface of the leaf appear to be recessive characters. Hairiness of the other leaf parts was intermediate in the hybrids studied.

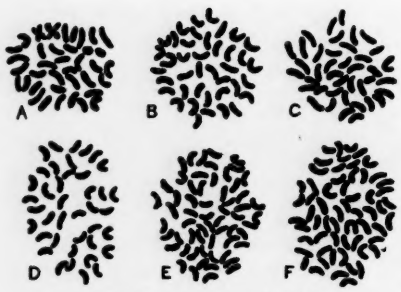
Floral Characteristics

A comparison of the floral characteristics of the three *Paspalum* species and their hybrids appears in Table II. Although the number of racemes per panicle in Table II, determined in late summer, is low for all plants, the relation between the parents and the hybrids is essentially the same as that occurring earlier in the season when a greater number of racemes per panicle was formed. Of the grasses included in this analysis, $V \times M$ No. 5 and the two $(V \times M) \times V$ hybrids produced significantly more racemes per panicle and Dallis grass significantly fewer racemes per panicle than the others.

The relative shape, size and hairiness of representative spikelets of the parents and their hybrids are shown in Figure 9 and are described in Table II. *P. malacophyllum* is the only *Paspalum* species in this region in which the second glume is absent. It is interesting to note that the second glume in the $V \times M$ hybrids was either absent like the male parent or greatly reduced in size. The fertile lemma of *P. malacophyllum* is very strongly nerved while the nerves on the fertile lemma of Vasey and Dallis grass are indistinct. The hybrids were intermediate in this characteristic. The purplish brown color of the *P. malacophyllum* spikelets, not characteristic of the other two parent species, appeared in the hybrid spikelets in proportion to the relative amount of *P. malacophyllum* germ plasm in the hybrid.

The anthers of Dallis grass are colored dark purple and the anthers of Vasey grass are pure yellow. The *Paspalum malacophyllum* anthers are red to reddish yellow on the broader surfaces and are yellow in the sutures between the pollen sacs. The anthers of the $V \times M$ hybrids were yellow with traces of red showing on the pollen sacs. The $(V \times M) \times D$ anthers were dark purple and the $(V \times M) \times V$ anthers were colored pure yellow.

Since species hybrids are usually sterile, it is not surprising that the anthers of the $V \times M$ hybrids have never dehisced or shed pollen. Considering this



PASPALUM CHROMOSOMES

Figure 10

Camera lucida drawings of chromosomes at the equatorial plate in cells from root tips of: *A—Paspalum malacophyllum, 2n* 40; *B—P. urvillei, 2n* 40; *C—P. dilatatum, 2n* 40; *D—P. urvillei* × *P. malacophyllum* No. 5, *2n* 40; *E—P. urvillei* × *P. malacophyllum* × *P. urvillei* No. 2-7, *2n* 60; and *F—P. urvillei* × *P. malacophyllum* × *P. dilatatum* No. 6-63, *2n* 60.

fact, however, a satisfactory explanation for the formation of some apparently viable pollen by the $(V \times M) \times D$ hybrids cannot be offered at this time. The magnitude of the standard error for the $(V \times M) \times D$ pollen grain diameters shown in Table II indicates that those grains that appeared to be viable varied much more in size than the pollen grains of the three parent species.

It is interesting that the anthers of the $(V \times M) \times V$ hybrids failed to shed pollen in 1940 but did so in 1941. This $(V \times M) \times V$ pollen was similar in size and quality to that produced by the $(V \times M) \times D$ hybrids. $(V \times M) \times V$ plants transplanted from the field to the greenhouse in the summer of 1941 for several weeks produced anthers which failed to shed pollen. Later these same plants produced pollen-shedding anthers. Thus it appears that the balance between male fertility and sterility in the $(V \times M) \times V$ hybrids is such that slight differences in the condition of the plant can make it male sterile or relatively male fertile.

Dry Matter Production

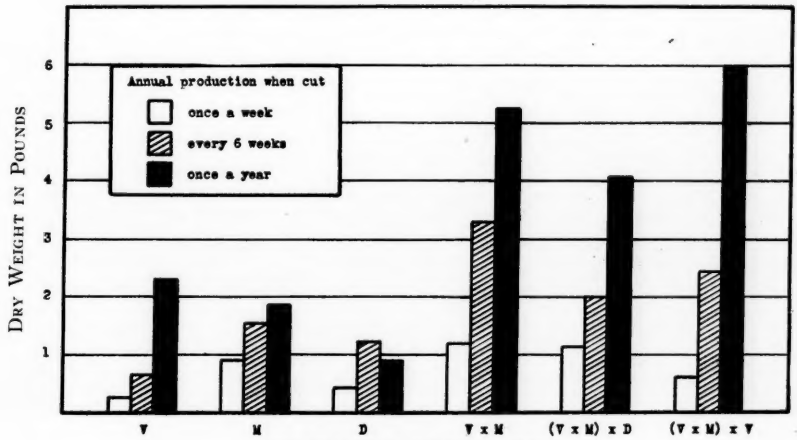
The analyses of variance of the total dry matter produced in 1940 and 1941 on each of the nine strains of grass carried at three fertility levels and given three clipping treatments has been calculated. Although all the sources of variation except the strains × fertilizer interaction were significant and exceeded the one per cent point, only those results dealing with the strains and their significant clipping interaction will be discussed here. A summary of these data is presented in Table III.

In light of the nature of this test the quantitative data presented here must be carefully interpreted. Observations of a number of specimens of each hybrid combination and species indicate that the clones chosen were fairly representative. Uniform clones were widely spaced and clean cultivated in an effort to avoid plant competition but the marked difference in the spreading characteristics of each, probably soon placed the bunch grasses at a disadvantage, most pronounced under frequent clipping. However, the data do furnish a good indication of how the parents and their hybrids may be expected to compare under different systems of management.

Table III shows that the three parent species responded to the different clipping treatments in much the same manner in 1940 and in 1941. The yields of dry matter indicate that *P. malacophyllum* is the most tolerant and Vasey grass the least tolerant of the parents to frequent close defoliation.

When cut but once, late in the fall of 1940 and 1941, the $V \times M$ and the $(V \times M) \times V$ hybrids produced over twice as much dry matter as Vasey grass, the highest yielding of the three parent species. These differences exceeded the 1% point. The $(V \times M) \times D$ hybrids, not significantly more productive than the parents in 1940, produced significantly more dry matter in 1941 and yielded over twice as much as Vasey grass. Thus it appears that these hybrids possess much hybrid vigor.

When clipped weekly the prostrate $V \times M$ No. 5 was the only hybrid in 1940 that significantly outyielded the best parent, *P. malacophyllum*. In 1941 both $V \times M$ and $(V \times M) \times D$ hybrids outyielded *P. malacophyllum* by a sub-



DRY MATTER PRODUCTION

Figure 11

The average 1940-1941 dry matter production of representative clones of *P. urvillei* (*V*), *P. malacophyllum* (*M*), *P. dilatatum* (*D*) and their hybrids when spaced eight feet by eight feet, April 26, 1940, and clipped at a height of four inches at different frequencies.

stantial margin. The more erect, bunch type $(V \times M) \times V$ hybrids were inferior to the other hybrids under this treatment.

When cut at six-week intervals, all of the hybrids produced more dry matter than the parent species in 1940 and 1941. However, only the $V \times M$ hybrids in both years and the $(V \times M) \times V$ 2-7 hybrid in 1941 yielded significantly more than *P. malacophyllum*.

In most instances both clones of each hybrid combination responded similarly to the various clipping treatments and yielded as much or more than the best species in the test. In an effort to demonstrate this point and show the comparative yield response of each species or hybrid combination in this test, the data in Table III have been combined and are presented graphically in Figure 11.

Seed Production

The total amount of good seed harvested from the three *Paspalum* species and their hybrids for the period August 14 to October 23, 1940, appears in Table IV. Seed production studies carried on for four years with several *Paspalum* species indicate that the percentage of florets containing caryopses and the total caryopses of Dallis grass and *Paspalum malacophyllum* shown in Table IV are below normal.

It is interesting to note that although the percentage of florets to set seed in all of the hybrids was much lower than in the parent species, the $(V \times M) \times V$ No. 2-7 hybrid produced as many grams of caryopses per plant as Dallis grass and *P. malacophyllum*. Although the $V \times M$ No. 5 hybrid and the two $(V \times M) \times V$ hybrids actually produced more caryopses during the period of this test than Dallis grass, they yielded only a calculated two to six pounds of viable seed per acre for the total period. Closer spacing of the plants might have increased this yield several times, but hardly enough to make the seed cheap enough to permit the propagation of the hybrids by common seeding methods.

In the analyses of variance of the percentage of florets to set seed, the *F*-value for the dates of harvest for the hybrids and their parents exceeded the 1% point, indicating that under the most favorable environment the seed production of the

FLOODING TOLERANCE

Figure 12

From left to right occur plants of *Paspalum malacophyllum*, *P. urvillei* × *P. malacophyllum* No. 3 and *P. urvillei* photographed after two weeks of flooding with water. Note the light colored leaves of *P. malacophyllum*, indicative of its inability to tolerate flooding.

hybrids as well as the parents might be increased materially. The significant differences in the percentage of florets to set seed obtained between the two representative plants of each of the three hybrid combinations suggest that other hybrids involving the same species may be found to be better seeders than the ones used in this test.

Ergot Resistance

The effect of ergot upon the yield and quality of Dallis grass seed is indicated by the studies made of the seed harvested from the Dallis grass plants in this test in 1940. An average of all of the harvests revealed that out of the 35.5 per cent by weight of florets left after the empty ones had been removed by blowing, only 39.0 per cent contained caryopses. The remainder of the heavy florets, 61 per cent, contained ergots. The Vasey grass in this planting developed few ergots except when inoculated artificially and no ergots could be found on the *Paspalum malacophyllum* plants whether naturally or artificially inoculated.

Our failure to find ergots on artificially inoculated heads of the two $V \times M$ hybrids indicates that they are immune to ergot and that ergot resistance is a dominant character. No ergot could be found on the $(V \times M) \times V$ plants without artificial inoculation and then only a trace of ergot appeared. Although few ergots appeared on the $(V \times M) \times D$ plants in this planting without artificial inoculation, when inoculated, or in other tests where Dallis grass furnished an abundance of inoculum, both hybrids developed a great many ergots. Nevertheless, they were unquestionably more ergot resistant than Dallis grass.

Heat and Drought Tolerance

If the ability to grow from August until October (usually the period of greatest heat and drought at Tifton) is an index of heat and drought tolerance, *Paspalum malacophyllum* ranked first and Dallis grass last among the parent species in 1940. In this test Dallis grass made little growth after the middle of August regardless of treatment and by October 30 practically all of the aboveground parts of the plants not clipped were dead, as evidenced by the 97.8 per cent dry matter content of the single harvest of that date (see Table I).

A leaf fungus (*Colletotricum graminicolum* (Ces.) Wils.) was found growing in abundance upon the leaves of these plants in the fall of 1940 and was probably one of the factors responsible for the failure of Dallis grass to grow in late summer and fall.

The relative dry matter production of the hybrids in terms of their *Paspalum malacophyllum* parent was calculated for each six-week harvest. These data revealed that each of the hybrids produced relatively more dry matter in the September 18 and October 30 harvests when compared with *Paspalum malacophyllum* than they did in the earlier six-week harvests. $V \times M$ No. 5 was outstanding in this respect.

Flooding Tolerance

Although Vasey grass frequently occurs on rather dry road embankments, it is best adapted to low wet areas and makes a very satisfactory growth in locations where water may stand for several weeks at a time. *P. malacophyllum* on the other hand is best adapted to well drained upland soils and attempts to establish it in poorly drained areas at Tifton have failed. Since the flooding tolerance of a grass determines the amount of drainage necessary for its culture, it is obviously a most important characteristic of lowland pasture grasses.

In order to better understand the inheritance of flooding tolerance the following greenhouse experiment was conducted. Five well established 6-inch glazed pots of Vasey grass, *P. malacophyllum* and of $V \times M$ No. 3 were flooded continuously for ten weeks while another five pots of the same grasses were maintained at an optimum moisture level by bringing them up to weight by the addition of water at daily intervals. The photograph in Figure 12 taken after two weeks of flooding, demonstrates the dominant nature of the genes controlling flooding tolerance in the $V \times M$ No. 3 hybrid.

In the last five-week period of the test the five flooded pots of Vasey grass produced as much dry matter as the five pots not flooded while the flooded *P. malacophyllum* plants yielded only one-fourth as much dry matter as the plants not flooded. At the same time the five flooded pots of $V \times M$ No. 3 yielded three-fourths as much dry matter as the pots carried at an optimum moisture level.

Frost Resistance

Temperatures of 25 degrees Fahrenheit on November 15, and 28 degrees on December 4 injured some of the hybrids and parents in this test much more severely than others. All of the plants in this study were rated from 1 to 10 on the basis of their injury following these frosts. A summary of these ratings revealed that Vasey grass and Dallis grass were the most frost resistant grasses in the test and were injured little by these temperatures. *Paspalum malacophyllum,* the most susceptible of all, was frozen back completely to the ground. The various hybrid combinations were intermediate in their frost resistance, the $V \times M$ hybrids being injured more than the $(V \times M) \times D$ and $(V \times M) \times V$ hybrids.

Observations made on the growth of these plants in the spring of 1941 revealed that Dallis and Vasey grass started to grow first, followed closely by the $(V \times M) \times D$ and $(V \times M) \times V$ hybrids. The $V \times M$ hybrids were noticeably slower than the other hybrids but started to grow earlier than *Paspalum malacophyllum.*

Cytological Investigations

Camera lucida drawings of the chromosomes at the equatorial plate in the root tips of the parents and some of the hybrids appear in Figure 10. As previously stated the three *Paspalum* species used as parents for these hybrids possessed 40 chromosomes as the $2n$ number. Five $V \times M$ hybrids, two of which were used in this test, all possessed 40 chromosomes as the $2n$ number. A number of equatorial plates in the root tips of ten of the $(V \times M) \times D$ tri-hybrids were examined cytologically and in all but one of the hybrids the $2n$ number was unquestionably

60 indicating that a chromosome set of each species was present. Although one equatorial plate of this exception was counted with 60 chromosomes several were found that seemed almost certainly to have several more than 60. The two $(V \times M) \times V$ hybrids used in this study possessed 60 somatic chromosomes indicating that they probably contained one set of *P. malacophyllum* chromosomes and two sets of Vasey grass chromosomes.

Progeny Studies

To answer in part a question that will no doubt be asked by many readers, a brief preliminary statement of the breeding behavior of these species hybrids and their parents follows. A more detailed report of this phase of the work will be presented later.

Studies of large populations of Dallis grass indicate that seedling plants may vary considerably in vigor and longevity but that they differ little if any in ergot resistance, all of those studied being very susceptible to this disease. With the exception of slight variations in plant size, 1,000 selfed seedlings of *Paspalum malacophyllum* were found in 1937 to be remarkably uniform. Some 7,000 selfed or open pollinated seedling plants of Vasey grass have been studied in the past few years. Although some variation in size and vigor was noted, all of the plants were very uniform in respect to their erect habit of growth.

The anthers of the $V \times M$ hybrids do not dehisce and no normal pollen grains (only a few aborted ones) can be found upon the dissection of the anthers. Studies of several hundred seedlings coming from seed produced on these $V \times M$ hybrids revealed that most of them were exactly like their parents morphologically. Since the cytological investigations proved that the $V \times M$ hybrids were not amphidiploids and since no self-pollen entered into the formation of the seeds from which these plants grew, it must be concluded that the $V \times M$ hybrids are reproducing by some form of apomixis. Whether or not the embryo arises by parthenogenesis, sporophytic budding or in some other manner awaits further cytological study.

Seedling progenies of a number of the $(V \times M) \times D$ hybrids have been found to be remarkably uniform and with very few exceptions appear to be exactly like their parents. Cytological studies proved that these $(V \times M) \times D$ hybrids are not amphidiploids. The anthers of these hybrids dehisce and shed some apparently viable pollen along with some that is aborted. The uniformity of the seedling progenies of these hybrids indicates that very little segregation is occurring and suggests that the pollen grains are probably not effective in fertilizing the eggs of these florets. Obviously the exact explanation of the mode of reproduction in these hybrids is dependent upon further cytological investigations.

Studies of seedling progenies of the $(V \times M) \times V$ hybrids are not sufficiently advanced to warrent comments upon them at this time.

Summary

In some 5,000 seedling plants of a single *P. urvillei* (V) plant grown some 50 feet from a planting of *P. malacophyllum* (M), five unusual plants, very similar to controlled $V \times M$ hybrids made more recently, were found. These hybrids were male sterile and when pollinated with *P. urvillei* (V) and *P. dilatatum* (D) pollen gave rise to 57 $(V \times M) \times V$ hybrids, 100 $(V \times M) \times D$ hybrids and several hundred plants identical with the female $V \times M$ parent.

The hybrids showed a great deal of hybrid vigor in a preliminary test and in most instances produced as much or more dry matter than the best parent species. When cut only once, in the fall, the hybrids produced over twice as much dry matter as their parent species.

In these hybrids varying degrees of dominance were observed in the expression of the following characters: glabrous over hairy, mature leaf margins and blades, complete; presence of the second glume over its absence, partial; glabrous over hairy glumes, partial; yellow over partial red anther color, partial; purple

over yellow and red anther color, complete; ergot resistance over susceptibility, complete in the $V \times M$ hybrids, partial in some $(V \times M) \times D$ hybrids; tolerance over intolerance of flooding, partial; and drought and heat tolerance as evidenced by ability to make good late summer and fall growth over intolerance, partial.

No evidence of dominance was noted in the inheritance of the following characters: hairiness of the sheaths or margins of the first seedling leaf, spikelet shape, glume color, prominance of nerves on the fertile lemma or resistance to frost injury.

Seedling progenies of some of the $V \times M$ and $(V \times M) \times D$ hybrids have been found to be remarkably uniform and with very few exceptions appear to be exactly like their hybrid parents morphologically.

All of the *Paspalum* species hybrids in this test were highly sterile. On the average the 1940 florets contained only 0.39 to 3.14 per cent of caryopses by weight, quantities too small to permit the propagation of these hybrids by common seeding methods.

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Table I. A comparison of the vegetative characteristics of three Paspalum species and their hybrids grown without plant competition in 1940.

Character Studied	D	M	V	V × M		(V × M) × D		(V × M) × V	
				S	S	7-42	8-83	2-4	2-7
Mature plant height in inches	28	36	64	42	34	34	40	55	54
Coarseness rating of mature stems *	3.0	5.0	1.5	3.5	3.5	3.0	3.0	1.0	1.0
Angle made by mature stems with the ground in degrees	20-45	70-80	30-90	45-60	30-45	35-45	40-50	60-80	60-90
Seasonal spread - diameter of rooted stems in inches	13.1	18.2	8.2	20.9	32.0	21.8	20.8	12.9	14.4
Succulence of plants cut once - per cent of dry matter	97.8	45.8	43.3	44.3	44.5	39.9	39.4	43.3	43.2
Hairyness of leaf parts *									
Sheaths of lowest leaves	3	1	1	1	1	2	2	1	1
Sheath of upper leaves	0	1-3	0	0	0-5	0-2	0-2	0-0	0-0
Leaf blade margin - first seedling leaf	0	1	0	3	3	0	0	3	3
Leaf blade margin - mature leaves	0	1	0	0	0	0	0	0	0
Upper surface of leaf blade	0	1	0	0	0	0	0	0	0

unless otherwise stated.

* The ratings on hairyness applies to the majority of leaves on mature plants. Plants rated No. 1 were very hairy or very coarse. The zero rating indicates the absence of hairs.

NOTE: The least significant mean difference between species for seasonal spread is 2.9 inches at the 5% point and for the per cent of dry matter as an index of succulence is 2.8 per cent at the 5% point.

Table II. A comparison of the floral characteristics of three Paspalum species and their hybrids grown without plant competition in 1940.

Character Studied	D	M	V	V × M		(V × M) × D		(V × M) × V	
				S	S	7-42	8-83	2-4	2-7
Racemes per panicle	4.0	8.3	8.1	9.4	11.8	8.0	7.0	11.8	10.8
Spikelet length in mm.	3.0	2.0	2.2	2.1	2.1	2.6	2.8	2.4	2.4
Spikelet width in mm.	2.2	1.0	1.2	1.1	1.1	1.5	1.5	1.2	1.2
Second glume of the spikelet	present	absent	present	absent or reduced		present		present	
Spikelet hairyness *	3	0	1	4	4	3	3	3	3
Anther color	purple	yel. & red	yellow	yel. with trace of red at the base		purple		yellow	
Dehiscence of anthers	yes	yes	yes	no	no	yes	yes	some	no
Viable pollen produced	much	much	much	none	none	some	some	** some	none
Pollen grain diameter in microns	37.0 ± 2.9	36.1 ± 2.7	37.5 ± 2.0			38.4 ±	3.5		

* Plants rated No. 1 were very hairy. The zero rating indicates complete absence of hairs.

** The anthers of these hybrids were never observed to dehisce or shed pollen in 1940. In 1941 they dehisced regularly and shed pollen similar in size and viability to that produced by the (V × M) × D hybrids.

Table III. The comparative annual dry matter production of three Paspalum species and their hybrids when clipped at a 4-inch height at different frequencies.

Species or hybrid	Annual mean dry matter production when cut					
	Weekly		Every 6 Weeks		Once in late Fall	
	1940	1941	1940	1941	1940	1941
	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.
Parents						
Paspalum urvillei (V)	.18	.36	.75	.61	1.92	2.67
Paspalum malacophyllum (M)	.70	1.14	1.05	2.10	1.83	2.23
Paspalum dilatatum (D)	.36	.81	.97	1.29	1.05	.77
Hybrids						
V × M No. 3	.96	1.57	2.02	4.48	4.13	6.40
V × M No. 5	1.03	1.58	2.41	4.29	4.03	6.47
(V × M No. 3) × D No. 6-83	.86	1.40	1.94	2.85	2.80	5.37
(V × M No. 5) × D No. 7-42	.81	1.94	1.50	3.02	3.00	5.47
(V × M No. 3) × V No. 2-4	.29	.84	1.32	3.11	3.40	6.37
(V × M No. 5) × V No. 2-7	.48	.87	1.57	3.73	3.40	6.67
Least significant 5% mean difference	.23	.40	.55	1.24	1.65	1.78

NOTE: Uniform clones of each grass were spaced 8' x 8' in the field on April 26, 1940. Three clones of each grass were subjected to each of the above clipping treatments.

Table IV. The total caryopses production of three Paspalum species and their hybrids from August 14 to October 29, 1940.

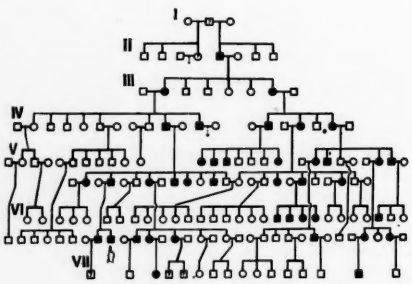
Species or Hybrid compared	Percentage by weight of florets containing caryopses	Total Caryopses Production per plant in grams	Weight of 100 Caryopses in grams	No. calculated caryopses produced per plant in 1940
Parents				
Paspalum urvillei (V)	88.70	34.98	0.070	499300
Paspalum malacophyllum (M)	16.23	4.21	0.042	10000
Paspalum dilatatum (D)	12.62	4.61	0.173	2665
Hybrids:				
V × M No. 3	2.77	0.46	0.053	868
V × M No. 5	1.52	1.59	0.053	3000
(V × M No. 3) × D No. 6-83	1.43	0.62	0.108	574
(V × M No. 5) × D No. 7-42	0.79	0.59	0.108	546
(V × M No. 3) × V No. 2-4	2.53	2.47	0.098	2540
(V × M No. 5) × V No. 2-7	3.14	4.53	0.094	4820

NOTE: The least significant mean difference between species for total caryopses production in grams is 1.65 grams at the 5% point. The least significant mean difference between the hybrids in percentage of florets containing caryopses is 0.52 per cent at the 5% point.

INHERITED FOOT-BLISTERING IN AN AMERICAN FAMILY*

INHERITANCE of foot-blistering during warm weather has been described in two families of London by Cockayne[1] and in a family of Wiltshire, England, by Haldane and Poole.[2] The family to be described here has lived in West Virginia for seven generations, and seems to have no connection with the English families. The affected members show blisters on the feet and hands, apparently quite like those of the other cases. The blisters resemble the watery eruptions typical of the dominant form of *epidermolysis bullosa,* but occur only on the feet and hands, only during warm weather, and then especially after unusual activity in walking or labor with hand tools. Sometimes they become bloody, and occasionally develop pus-forming infections. There is no record of such concomitants of *epidermolysis bullosa* as permanent scarring, dystrophy of the nails, or dermatographia. The blistering is said to show differences in intensity among the affected individuals. The first person shown as affected in the chart (Figure 13) is said to have "spent most of the summer, seated in a rocking-chair, with his hands and feet almost completely covered with blisters." However, it is less severe in the later generations, and the propositus considers his case to be rather mild. The tendency to blister seems to decrease as the subject grows older. The father of the propositus, now past 50, thinks that he suffered more when he was about 25 years old, and one of his brothers gives the same report.

The first male shown in the chart (I-2) is Zachariah Piles, born 1762, and settled in western Virginia in 1780. He probably had the foot-blistering character, since it is family tradition that some of the children of his first wife and some of their descendants showed the trait, and the inheritance of the character through the descendants of his second wife is shown in the chart. There are 40 cases, and each affected person, except the first one, is known to have had an affected parent. Twenty of the affected are males, and 20 females, and altogether they have 32 normal sibs. The children of affected parents include 39 affected, 38 normal, and 3 who, because of extreme youth, are marked questionable. The inheritance thus seems to be due to a single autosomal factor. Since it is not known in the homozygous state, it must be called a conditional dominant.



FOOT-BLISTER PEDIGREE
Figure 13
Six generations of inheritance of a tendency to form blisters on hands and feet.

We are indebted to Mrs. Mary Fetty Cordray and to Mrs. Elizabeth Fetty for additional information and for checking a portion of the chart, and to Earl L. Core for his interest and assistance furnished by his local history.[3]

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BOWED PASTERN IN JERSEY CATTLE

F. W. Atkeson, Franklin Eldridge and Heman L. Ibsen

An anomaly consisting of a malformation of the rear pastern joint was observed on registered Jersey cattle in five widely separated herds. The cattle in three of the herds were not related to cattle in the other herds, while in two herds some similarity of bloodlines existed. Sporadic cases of the malformation have been noticed in other Jersey herds and in Holstein herds, but no data on the prevalence of the character in various breeds of cattle are available.

In bowed pastern the affected pastern joint does not line up the hoof and cannon bone but instead appears to bow outward causing the foot to set on the ground at an inward angle (Figure 14). Since there has been no opportunity to dissect a typical bowed pastern, exact description of the anatomical derangement is impossible. The lateral and medial digits appear to be spread more widely than normal. Whether the bowing effect is caused by one or more of the lateral phalanges being longer than normal, or the medial phalanges being shorter is not known. Extreme cases appear to have bony enlargements at the junctions of the phalanges.

In the first herd observed, a number of affected animals were by the same sire: and in the second herd two extreme cases were full sisters. These observations suggested that the character might be hereditary. When 16 positive cases and 11 questionable cases were observed in a herd of 102 cattle of known ancestry, an attempt was made to trace the inheritance of the character.

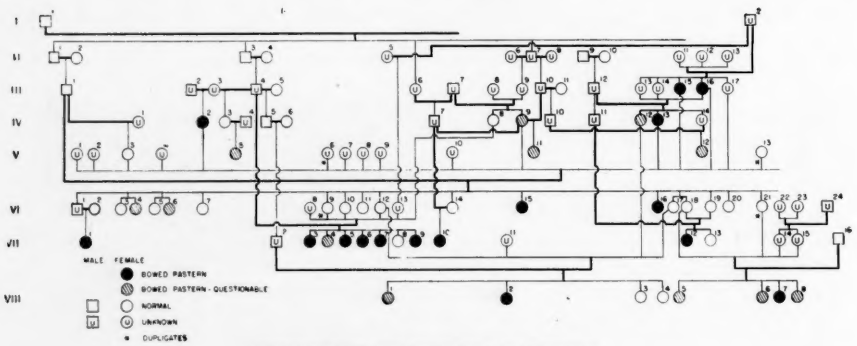
Expression of the character varies in degree from pronounced cases to those difficult to distinguish from normal. Experienced cattle breeders seem unfamiliar with the character and are surprised to have cases pointed out in their own herds. They can readily detect all but questionable cases after the character is called to their attention. Although the character is more readily noticed in adult animals, particularly in slight cases,

BOWED PASTERNS

Figure 14

Two views of an extreme case of bowed pastern. Both pasterns were affected but the left was much worse than the right.

*Contribution No. 149 from the Department of Dairy Husbandry and No. 150 from the Department of Animal Husbandry, Kansas State College.



PEDIGREE OF BOWED PASTERN

Figure 15

Occurrence of the bowed pastern character in eight generations of matings in one herd of Jersey cattle.

there is no doubt that the animals are born with the defect. Selection against the malformation, if any, has undoubtedly been limited.

Figure 15 shows that this anomaly positively occurred in two consecutive generations. Of the 16 sires represented on the pedigree chart, 10 had one or more offspring definitely showing the character, and five other bulls had one or more daughters in which the identification of the deformity was questionable. The fact that there were 16 positive cases and 11 questionable cases, making a total of 27 animals possibly affected among a total of 102 animals observed, indicates a rather wide distribution of this character through the herd. Since the bowed pastern character has been observed in other herds, it is not peculiar to the herd studied and further investigation may prove it to be generally disseminated through the breed.

That the character is hereditary is supported by the frequency of occurrence, the relationship of affected animals within a herd and the preponderance of affected animals among the progeny of certain sires. That the deformity is not the product of nutritional disturbance is indicated by the fact that normal animals were grown under similar conditions. Furthermore, one bull sired affected offspring in two herds, the second being a well fed college herd in which the character had not previously been observed. From available data it is not possible to postulate a theory of the mode of inheritance of this character. Results of matings shown in Figure 15 could be explained equally well on the basis of a single dominant or a recessive factor.

✦

An Activity-Gene in the Albino Rat

The genetic differences between the two strains as indicated by the activity of animals derived from the various cross matings cannot be attributed to multiple factors. The inactive backcross males are as inactive as males from the true inactive strain and the active backcross females tend to be as active as females from the true active strain. These results as well as the clear cut segregation which occurs among both generations of active backcross males and the second generation of inactive backcross females support the hypothesis that a single gene pair is involved in which the inactive component is dominant in the males and recessive in the females. The effects of this gene, however, are evidently not invariable. The difference between the two groups of F_1 males illustrates the marked variation which can occur when the gene pair is in heterozygous condition. Undoubtedly a similar type of variation accounts for the fact that segregation is masked in some of the crosses but appears in others.—Brody, E. G. Genetic Basis of Spontaneous Activity in the Rat. *Comp. Psych. Monographs.* August, 1942.

STUDIES OF QUADRUPLETS

V.—The Kaspar Quadruplets

IVA C. GARDNER AND H. H. NEWMAN

THE present paper deals with the fourth set of American quadruplets to be studied and analyzed by us and to be published in this JOURNAL. The Kaspars are diagnosed by us as a two-egg set, consisting of one-egg triplet boys and a girl sibling. This is the second two-egg-quadruplet set in our series, the first being the Badgett quads, recently written up in this JOURNAL. Of the four possible sex-distribution types (♂♂♂♂, ♀♀♀♀, ♂♂♂♀, ♀♀♀♂) the Badgets are examples of the second and the Kaspars of the third. It is probable that these four types occur with equal frequency. The hypothetical type (♂♂♀♀) consisting of two pairs of one-egg twins has never been reported.[2]

The Kaspar quadruplets were born May 9, 1936, in the Passaic General Hospital, Passaic, N. J. The mother was 36 years old at the time of the birth and the father ten years older. The parents are both German emigrés and the father a mechanic by trade. There are two older children, a boy of six and a half and a girl of eight years when the quadruplets were born. The quads consist of three boys, extremely similar in appearance, and a girl. The birth order was Frances, Frank, Felix and Ferdinand. We have no information as to the placenta and fetal membranes.

When the quadruplets arrived, the family income was very small and the sudden addition of four more children threatened financial disaster. Help, however, was forthcoming from the mayor of Passaic, who secured for the family several advertising contracts which have considerably improved their circumstances. It is thought that the world-wide publicity achieved by the Dionne quintuplets had much to do with increasing the interest of advertisers in this as in subsequent quadruplet births. The family income from advertising contracts has enabled the Kaspars not only to purchase the home they now occupy but has improved their situation in many other ways.

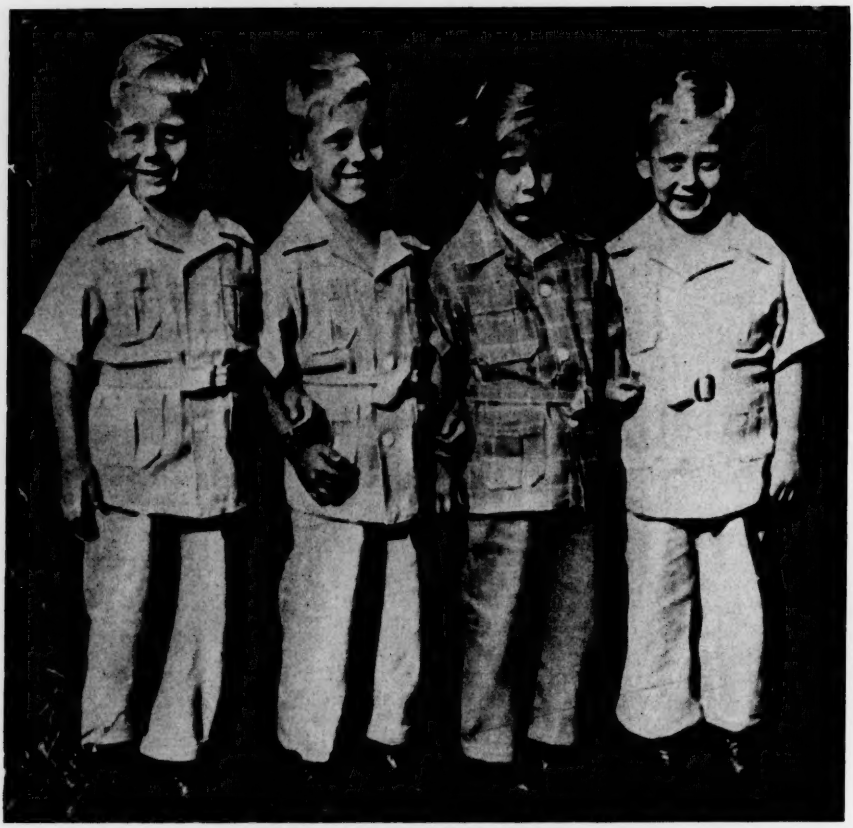
The Kaspar quads, like all other sets of quadruplets of which we have a record, were born prematurely. Their birth weights were as follows: Frances, 3 lbs. 11 oz.; Frank, 3 lbs. 12 oz.; Felix, 2 lbs. 13 oz.; and Ferdinand, 3 lbs. 10 oz. Felix, though much the smallest and least well developed at birth, is now somewhat larger and sturdier than Ferdinand. All of the quads are described by Dr. Gardner as "the sturdiest, huskiest set of quads I have ever seen." They were, when examined, all about equal in health and vigor and as well developed for their age as were the older brother and sister. The photographs (Figures 16-17) show the strong similarity of the three boys.

Dermatoglyphics of the Kaspar Quadruplets

In contrast to the case of the Badgett quadruplets, in which the prints were unsatisfactorily printed and did not afford in themselves very clear evidence of the zygosity of the set, the prints of the Kaspar quadruplets are moderately well made and would, in the absence of any other data, afford conclusive evidence that the set is a two-egg set (See Figures 18 and 19). The only defect in the whole set of prints is that the finger prints were not separately rolled and therefore do not permit accurate ridge counting.

Palm-Prints

	Left palm	*Right palm*
Frank	11.9 .7 .5′-tt′-L^{r}.O.O.L.O	9.9 .5″.5′-t″-A^{r}.O.O.L.O.
Ferdinand	9.7 .5″.2 -tt″-L^{r}.O.O.O.L	9.X .5″.4 -t″-A^{r}.O.O.V.O.
Felix	9.X.5″.4 -t″ -L^{r}.O.O.V.O	11.9 .7 .2 -t″-A^{r}.O.O.L.O
Frances	7.7 .5″.2 -tt′ -W^{r}.O.O.O.L/D	7.5″.5′ .4 -tt′-L^{r}/L^{u}.L^{c}.O.O.L



KASPARS AS FIVE-YEAR-OLDS

Figure 16

Ferdinand, Felix, Frances and Frank on their fifth birthday. The three boys are identical triplets; the girl merely a "sister." This three-and-one arrangement is the usual pattern among two-egg quadruplets.

It will be noted that all three boys have highly similar hypothenar radial loops on their left palms and equally similar radial arches (rather rare patterns) on their right hands, while the sister has a large radially twisted hypothenar whorl on the left palm and a compound twisted double loop on the right palm. It will also be noted that the main line pattern of Frank's left palm tends to be the mirror image of that of Felix's right palm, while the main lines of the left palm of Felix almost exactly mirror-image those of the right palm of Ferdinand. Taking the main lines and patterns together, however, the three right palms of the boys are more alike than any right palm is like

Finger-Prints

	Left hand					*Right hand*				
Frank	U.	W.	W^{lu}.	W^{lu}.	U	W^{lu}.	W.	U.	W^{lu}.	W^{lu}
Ferdinand	U.	W^{u}.	W^{u}.	W^{lu}.	W^{lu}	W^{lu}.	W^{lr}.	W^{lu}.	W^{lu}.	U
Felix	W^{lu}.	W^{lu}.	W.	U.	U	U.	W^{lr}.	W^{lu}.	W^{lu}.	U
Frances	A.	U.	U.	W^{lr}.	U	U.	U.	A.	A.	U

PIANO-PLAYING QUADS

Figure 17

The Kaspars take part in a radio program; they are all reported to be musical. Frances is at the left, and the three remarkably similar boys at the right.

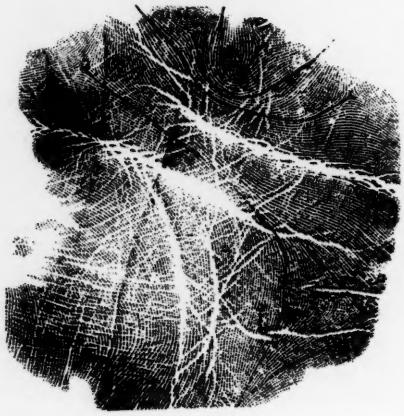
the left of the same individual. The same is true of the three left palms. This type of homolateral resemblance is generally regarded as strong evidence of monozygosity for twins and higher multiple births and here strongly points to the monozygosity of the three boys. This conclusion is reinforced by the fact that in almost every respect the palms of the sister differ materially from those of any of the boys.

It will be noted that in the three boys twisted whorls of several varieties are present on at least six of the ten fingers of each individual (in Frank there are seven such whorls and in Ferdinand there are eight). The two most similar hands, as was the case with the main line palm patterns, are the left hand of Felix and the right hand of Ferdinand, these two sets of finger-prints being not only mirror-imaged in general pattern types but in finer details. Next closest in resemblance among the eight hands are the left of Ferdinand and the right of Felix. The left hand of Frank is also more like the right hand of Felix than like his own right hand. In general, all of the finger patterns of the three boys are well-developed with moderately high

FRANCES (left)

FRANCES (right)

FELIX (left)



FELIX (right)

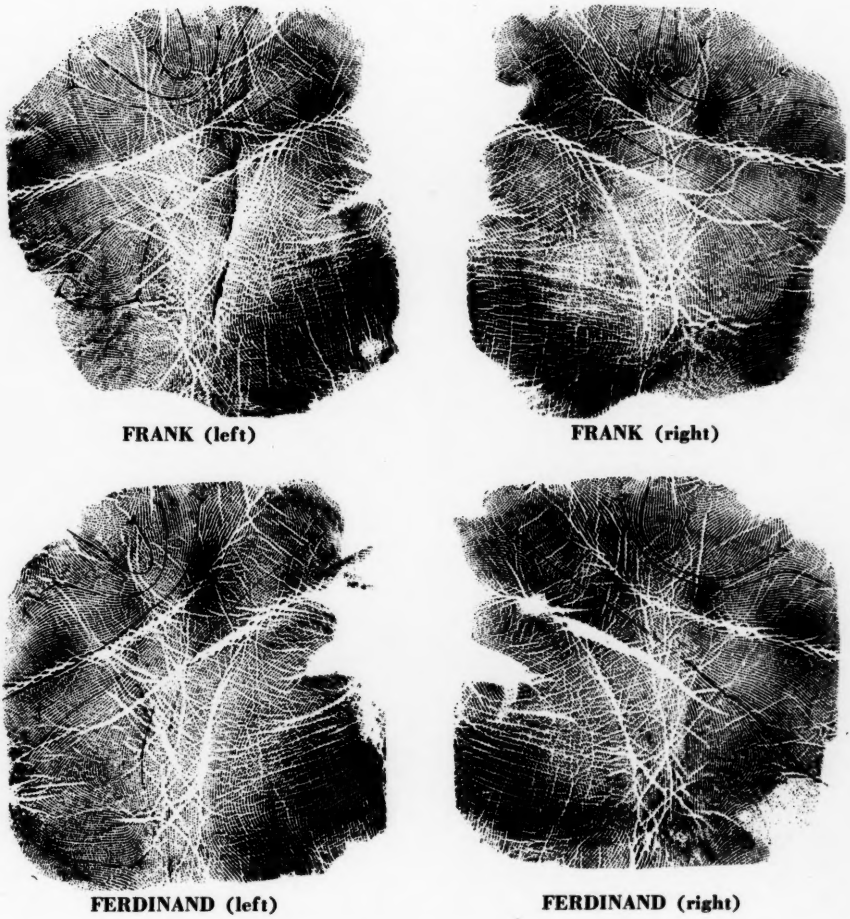
QUADS' PALM PRINTS

Figure 18

On the basis of palm prints alone it would have been possible to have diagnosed the zygotic pattern of the Kaspar Quads. Frances, the girl, has a very different pattern from her three brothers, whose main patterns are remarkably similar with striking mirror imaging.

ridge counts, some of the patterns being so large as to be partly excluded from the prints. In marked contrast to this, all of the finger patterns of Frances are of the most reduced type, consisting of one almost vestigial whorl, six very flat loops and three arches. The inter-resemblances among the three boys are emphasized by the marked contrast between the finger-prints of the girl and those of the three boys.

Had we been presented with nothing but the palm and finger-prints of this set of quadruplets and asked to make a diagnosis of their zygotic origin, we would unhesitatingly have adjudged the set to be a case of two-egg quadruplets consisting of a set of one-egg triplets and a "sibling." This diagnosis would be strongly reinforced by a study of the physical correspondences of the three boys as shown in Table I. These boys are all as similar to one another as the average pair of one-egg twins, but Felix



FRANK (left) **FRANK (right)**

FERDINAND (left) **FERDINAND (right)**

PALM PRINTS OF FRANK AND FERDINAND
Figure 19
The principal diagnostic pattern outlines are strikingly similar.

TABLE I. Physical Characters of the Kaspar Quadruplets.

Character	*Frances*	*Frank*	*Felix*	*Ferdinand*
Standing height	110 cm.	110 cm.	110.5 cm.	111 cm.
Sitting height	58 "	62 "	60 "	63 "
Head length	17 "	16.6 "	17.2 "	17.5 "
Head width	13 "	12.3 "	12.7 "	13 "
Eye color	blue with brown flecks	blue	blue	blue
Hair color	light, but darker than boys'	light	same as Frank	same as Frank
Skin color	fair, but slightly darker than boys'	more like Frances' than other boys'	fair	fair

and Ferdinand are so extremely similar that even their mother has difficulty in distinguishing them. Frank is only a little less similar to the two other boys, but as much like them as one-egg twins usually are like each other.

Without any knowledge of the placental relations, we can only guess at the embryonic history of this set of quadruplets. Our guess is that the first of the two zygotes to reach the uterus and to become implanted was the Frances zygote, that the second zygote was delayed in implantation and as a consequence underwent an early division into twin primordia, and that later one of these twin primordia divided again to form a secondary pair of twins. Since mirror imaging is strongest between Ferdinand and Felix it is our guess that these two are the product of the later twinning division.

The fetal membranes of the Kaspar quads were not available, but internal evidences from birth order, degrees of resemblance and mirror imaging, suggest that the placenta may have been much like that of the Badgetts, a trichorionic one with Frances having a separate placenta, with Felix and Ferdinand in a common chorion and Frank in his own chorion, but all three boys attached to a common placenta.

Mental and Personality Traits

On the somewhat hurried visit by Dr. Gardner to the home of the Kaspar quadruplets only one mental ability test was given, the Stanford-Binet Test, Form L. This test was given on August 28, 1940, when the quads were four years, three months old. The results of this test are as follows:

	Mental Age	*I.Q.*
Frank	4 years	94
Ferdinand	4 years	94
Felix	4 years	94
Frances	4 years, 1 month	96

The exact equality of the three boys is impressive. Even Frances is almost the same in mental ability as the boys, but seemed a shade brighter. Two facts help to account for the slightly below average ranking of these children: first, that they were premature and therefore not developmentally as old as their age dated from birth; second, they speak German in the home, while the test was administered to them in English, a language somewhat foreign to them. Only when they have gone to school and become more accustomed to English can we expect them to show their real ability on tests designed for rating American children.

With respect to personality traits, the Kaspar quads seemed to be all normal, rather noisy and active children. There seemed to be a strong feeling of unity among them, since any offense to one of them is taken as an offense to all and they band together to protect each other. Frances seemed to be the leader and was somewhat stronger than any of the boys. Felix is regarded by the parents as a little smarter than the other boys and Frank as not quite so smart as the other two, but the difference is not obvious to the outside observer. Frank seemed to Dr. Gardner to be a little quieter than the others, to enjoy playing alone more than the others did.

Summary

The Kaspar quadruplets are definitely diagnosed by us as a two-egg set. In this case the palm and fingerprints alone would have been sufficient for a zygotic diagnosis. The Kaspars differ from the Badgetts in being a mixed-sex set, three boys and a girl. The chances are equal that the single "sibling" accompanying three-egg triplets will be of the same or of opposite sex.

We regard the type of two-egg quadruplets represented by these two sets, Badgetts and Kaspars, each consisting of a set of one-egg triplets with a "singleton sibling," as probably the only kind of two-egg quadruplets that actually occurs.[2] It seems very unlikely to us that more than one egg in any plural-egg pregnancy ever undergoes one-egg twinning.

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